

ULTRASTRUCTURE OF *SYNORISPORITES DOWNTONENSIS* AND *RETUSOTRILETES* CF. *CORONADUS* IN SPORE MASSES FROM THE PŘÍDOLÍ OF THE WELSH BORDERLAND

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ABSTRACT. Scanning and transmission electron microscopy has been employed to describe the ultrastructure of constituents of two kinds of spore masses recovered on bulk maceration of basal Downtonian (Přídolí, Silurian) sedimentary rocks from the Welsh Borderland. Spores of *Synorisporites downtonensis*, occurring as tetrads in narrow, elongate masses, possess a thick homogeneous exospore. Adjacent tetrads are linked by sporopollenin bridges. Variation in distal sculpture is discussed in relation to spore ontogeny. Discoidal masses contain *Retusotriletes* cf. *coronadus* also isolated from coeval *Pertonella dactylethra*, the sporangia of which are of similar shape to those of *Cooksonia pertoni* and also terminate smooth isotomously branching axes. However, differences in ultrastructure of exospore, that in *R.* cf. *coronadus* shows faint striations, with a darker layer bordering the lumen, compared with the bilayered exine of *Cooksonia* spores, suggest that the two megafossil species are not closely related.

RECENT studies describing spores from a number of late Silurian and earliest Devonian plants have begun to demonstrate the potential of spore features as useful taxonomic characters in plants of simple morphology, when preserved as small coalified fragments (Fanning, Richardson and Edwards 1991; Edwards *et al.* 1994). In the case of *Cooksonia pertoni* Lang, 1937, sporangia have been shown to contain one of four taxa of dispersed spores that are similar in their equatorially crassitate structure and bilayered exospore, but differ in their distal sculpture (Fanning *et al.* 1988; Rogerson *et al.* 1993; Edwards *et al.* 1995). Here we extend our ultrastructural studies to *Synorisporites downtonensis* Richardson and Lister, 1969, the genus being recorded (as *S. verrucatus*) in *C. pertoni* subsp. *synorispora*, and to *Retusotriletes* cf. *coronadus*. The latter occurs in *Pertonella dactylethra* Fanning, Edwards and Richardson, 1991, a rhyniophytoid with sporangia identical in shape to those of *C. pertoni*, but bearing prominent spines (Fanning, Edwards and Richardson 1991).

LOCALITY DATA

1. Ludford Corner

Platyschisma Shale Member, Downton Castle Sandstone Formation, Přídolí Series. Eight elongate spore masses comprising *Synorisporites downtonensis* were picked out following bulk maceration of a siltstone layer 1.6 m above the top of the main bone bed at this famous locality in the small cliff at the junction of Ludford Lane (Whitcliffe Road) and Leominster Road (A49), c. 75 m south-south-west of Ludford Bridge, Ludlow [SO 5122 7412] (White and Lawson 1989). The exact location of a further three is less secure, but probably is at the same level or just below it.

2. Weir Quarry

Platyschisma Shale Member, Downton Castle Sandstone Formation, Přídolí Series. A single specimen with *Synorisporites downtonensis* was isolated from a siltstone clast c. 35 mm above a bone

bed (possibly equivalent to the main Ludlow Bone Bed) from an overgrown quarry *c.* 275 m north-east of Bringewood Forge Bridge, Downton Castle Estate, near Ludlow [SO 4560 7525] (Richardson and Rasul 1990).

3. *Perton Lane*

Rushall Beds (equivalent in the Woolhope Inlier of the Downton Castle Sandstone Formation), Přídolí Series. Two spore masses with *Retusotriletes* cf. *coronatus* were isolated from a buff, fine-grained micaceous sandstone just above a bone bed thought to be equivalent to the Ludlow Bone Bed at Ludford Lane. The horizon is in a small cutting on the eastern side of the lane leading to Perton Quarry, Stoke Edith, and to Copgrove near Hereford [SO 5971 4035] (Squirrell and Tucker 1960).

Spore assemblages from the horizons yielding spore masses at all three localities belong to the *Synorisporites tripapillatus* – *Apiculiretusispora spicula* Assemblage Zone (Richardson and McGregor 1986) which encompasses the base of the Downtonian and is considered equivalent to the lower part of the Přídolí Series.

TECHNIQUES

Conventional procedures for preparation of palynological samples were employed, except that centrifugation was omitted. Spore masses were picked out under a dissecting microscope, mounted on stubs, air dried and coated for SEM (Cambridge 360). One specimen from each locality was then prepared for TEM (Rogerson *et al.* 1993; Edwards *et al.* 1995). It was first divided into three, and a part mounted for light microscopy (LM). Prior to embedding and sectioning, one of the remaining fragments was treated with fuming nitric acid. Qualitative X-ray (energy-dispersive) microanalysis capable of detecting elements above sodium (atomic number 11) was employed on semi-thin sections of spores with blue-green interference colours using a Philips 300TEM. All stubs, grids and slides are housed at the National Museum and Gallery of Wales. Additional SEM images collected via a PC-based image capture and storage system are stored on hard disc (WORM drive). Selected images will be transferred to CD-ROM (durable non-fading format not subject to accidental erasure) to be deposited with the specimens.

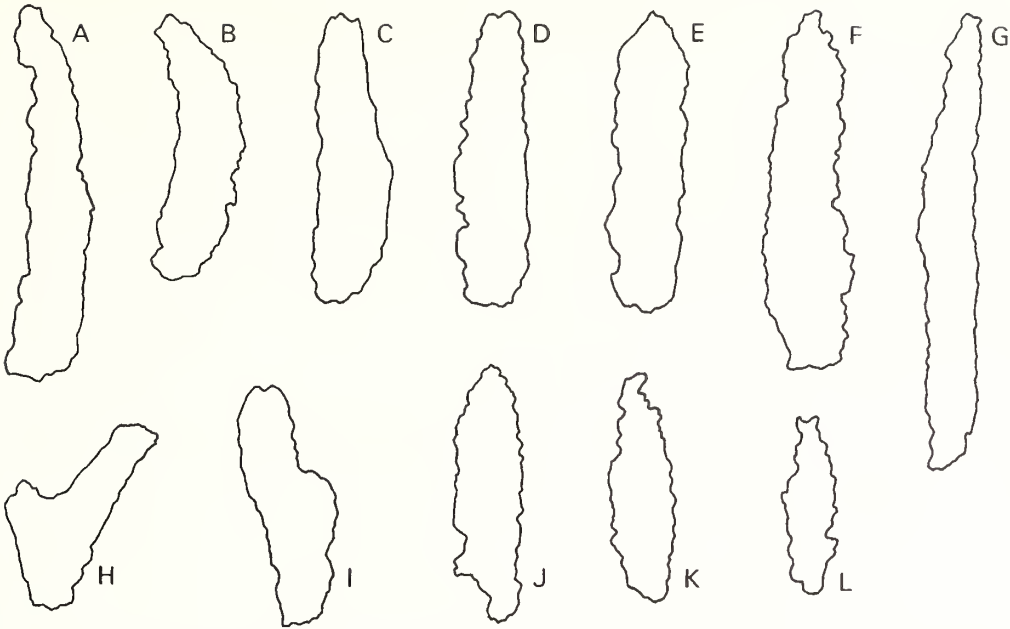
Terminology. This follows earlier usage (Rogerson *et al.* 1993) where the presumably sporopollenin-impregnated, acetolysis-resistant spore wall is called the exospore (\equiv exine).

SPORE MASSES WITH *SYNORISPORITES DOWNTONENSIS*

Description

SEM observations. Very narrow elongate spore-masses recovered from Ludford Lane (11) and Weir Quarry (one) are unusual in that the spores occur in tetrads (Text-fig. 1; Pls 1–3). Such masses range from 543 to 1490 μm long and 158 to 289 μm maximum width. They were probably circular in cross section with a maximum of 6 tetrads/diameter. Plate 1, figure 4 shows a typical representative with a tapering, probably complete rounded end while the other is irregular, truncated and probably fractured. The lateral contours are slightly and irregularly undulating except where tetrads are missing (Pl. 1, figs 3, 5). One example is bifurcated (Pl. 1, fig. 6). In a few cases, irregular fragments of a sheet-like material adhere to peripheral tetrads (Pl. 1, figs 7–8). This is interpreted as the remnants of a sporangial wall. It is usually a single, somewhat shredded layer with no indications of organization, with the possible exception of the fragment illustrated in Plate 3, figure 5 (arrowed).

The exposed distal surfaces of the spores are ornamented by muri (Pl. 1; Pl. 2, figs 1–9) except near the equator which is usually smooth. The width and prominence of this equatorial border varies between spore masses as do the shape, dimensions and resulting relief of the ornament. In many



TEXT-FIG. 1. Outline of elongate spore masses containing *Synorisporites downtonensis*. All from Ludford Lane, except G which is from Weir Quarry. A, NMW95.19G.1; B, NMW95.19G.5; C, NMW95.19G.2; D, NMW95.19G.12; E, NMW95.19G.13; F, NMW95.19G.3; G, NMW95.19G.7; H, NMW95.19G.6; I, NMW95.19G.9; J, NMW95.19G.4; K, NMW93.143G.8; L, NMW95.19G.8. All $\times 40$.

examples with well-defined ornament, the tetrads are connected by 'bridges' extending between usually distal peripheral muri (Pl. 3, figs 9–10). No such junctions occur in the tetrads of one specimen where the ornament is least developed and marked by sinuous grooves (Pl. 2, fig. 3) such that the surface appears flattened to slightly undulating. Gentle prodding with a needle usually separated the tetrads into individual components and revealed conspicuous triradiate folds, with interradiate irregular muri on the proximal surface giving a puckered effect (Pl. 2, figs 10–12; Pl. 3, figs 1–3). Muri may be absent near the proximal pole (Pl. 3, fig. 3) in some spores. Fortuitous separation of a tetrad shows continuity between the irregular proximal muri of adjacent monads (Pl. 3, fig. 7) although in others the proximal faces are completely separate (Pl. 2, fig. 11), the tetrad forming a hollow sphere of almost lenticular spores. An equatorial thickening cannot be distinguished in SEM, but this region appears to form a rigid marginal equatorial feature, sometimes accentuated by some inward collapse of the proximal surface but usually more sharply delimited on the distal. Further evidence for this comes from the more or less circular cracks on distal surfaces in one specimen (Pl. 2, fig. 3) where it is postulated that final stages in sporopollenin deposition have not been completed (see later). Such cracks are typically produced by radial stress during shrinkage with fracture occurring along weaker areas, in this case close to the inner limits of the marginal band. In all specimens the trilete mark is represented by a triradiate narrow fold, straight or slightly sinuous (Pl. 3, figs 1–3), extending to the equatorial feature.

Dimensions of sporangial masses and spores are given in Table 1. In some masses, the tetrads appear almost uniform in size and spherical in shape (Pl. 1, fig. 2), and are usually loosely packed. Where more variable in size, this is not gradational along the mass. Differences in appearance result from depressions in tetrads (either at the junction between three spores (Pl. 2, fig. 8) or on distal surfaces (Pl. 2, fig. 7)), degree of separation and sometimes slight overlap of the tetrad components (Pl. 2, fig. 9). Variation in distal ornament may relate to developmental stage (see later).

TEM observations. Sections are similar with and without fuming nitric acid treatment in both samples, with the 'best' sections from the Ludford Lane material. Their most distinctive features are the thick homogeneous exospore, electron-dense bodies in the lumen and the complete absence of any extra-exospore material. The exospore is conspicuously thicker in distal rather than proximal walls, with spore orientation determined by size and nature of ornament in section (Pl. 4, figs 1–4). There is little variation in total thickness of the distal wall, but in some sections, the proximal wall shows increase in width at the periphery of the spore (Pl. 4, fig. 3). Otherwise there is no pronounced equatorial thickening. Structurally the exospore appears uniform except at its inner and outer limits. Differences in intensity and extent of staining (minus acid treatment) in the outermost exospore in four spores from Ludford Lane shown in Plate 4, figures 2–9, 11–13 furnish inconclusive evidence for a very narrow (*c.* 1.2 μm wide) outer layer. Well-defined superficial layering is also present in some Weir Quarry spores. In one of two examples showing reversed staining (Pl. 4, fig. 10) this might reflect increased physical resilience (probably due to greater reinforcement by resin), because the rest of the spore has puckered/shattered on sectioning.

The innermost layer is of variable thickness, may be separated from the rest of the exospore by small voids (Pl. 4, figs 11–13) or may show further layers to the inside (Pl. 4, fig. 11). In the latter example, this might reflect the remains of spore contents sandwiched between proximal and distal wall inner layers, especially as the darkly staining elliptical bodies may also be so enclosed (Pl. 4, figs 11–12). Plate 4, figure 13 shows an example where these bodies of variable shape and size occur in a lighter homogeneous matrix filling the lumen of the cell. In a similar example from Weir Quarry, the darker bodies are surrounded by voids and more disorganized material which stains similarly to or less densely than the exospore. In other cases the lumen is marked by a space lined by the dark bodies. The nature of the innermost wall layer, be it part of the exospore, endospore or remains of spore contents, remains conjectural. The darkly staining bodies were originally thought to be pyrite, but this is unlikely as they survive nitric acid treatment. Traces of iron and sulphur along with silica and chlorine (from resin) were recorded in X-ray microanalysis, with highest peaks identified as tin (from the grid) copper (specimen holder) and calcium (?indigenous).

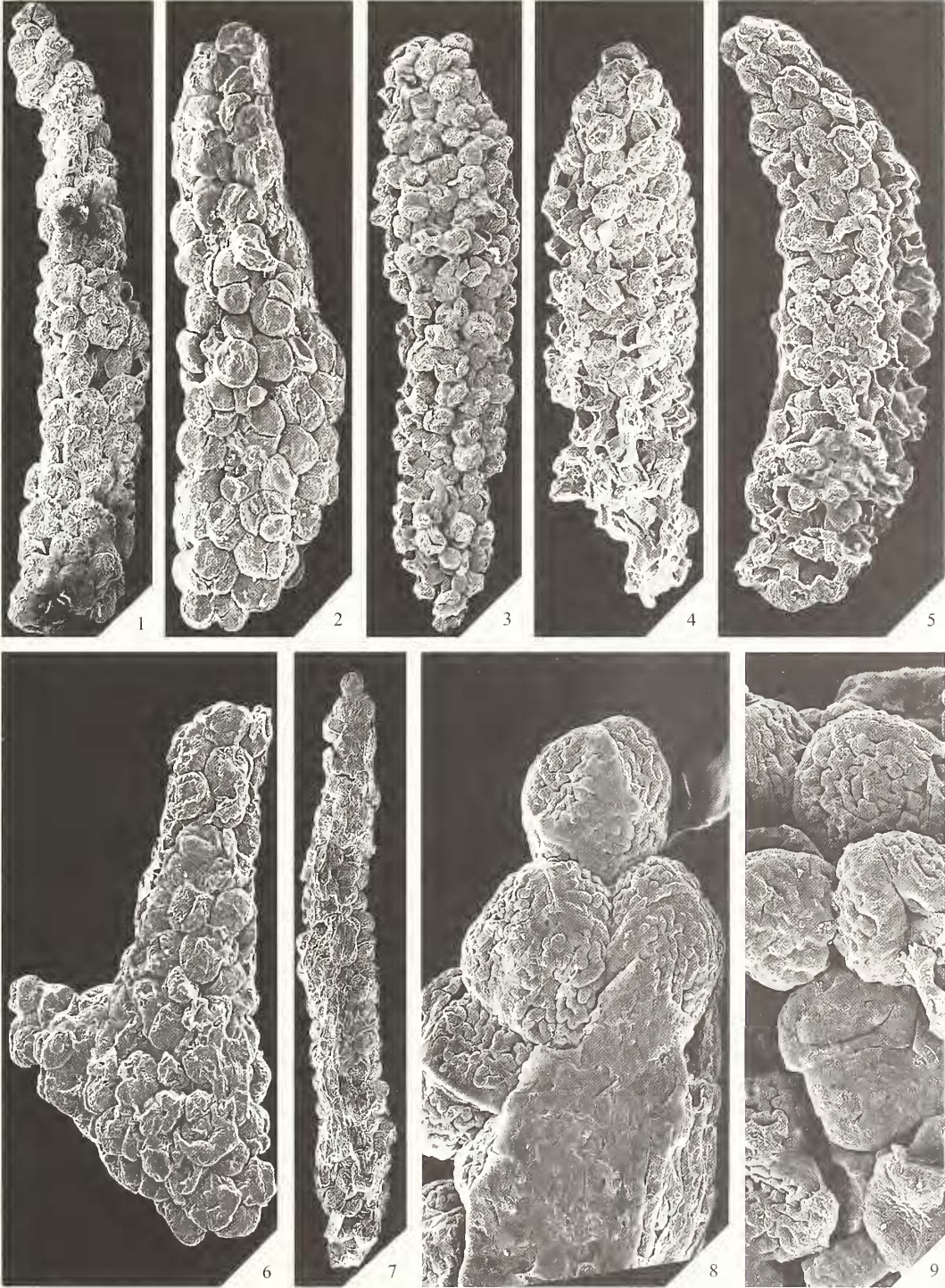
Distal ornament produces an undulating surface contour with more or less smooth curves (Pl. 4, figs 2–3), both higher and wider in cross section than the proximal, where the outline is more angular and less regular, sometimes almost serrated (Pl. 4, figs 3–4). Connections (bridges) between ornament in adjacent proximal faces in the same tetrad (Pl. 4, fig. 3) and distal faces of adjacent tetrads (Pl. 4, fig. 4) show no variation in ultrastructure, nor junctions. The illustrated section through a triradiate mark is tangential and probably close to the equator (Pl. 4, fig. 1). The apertural fold in SEM is seen in this LM section as a triangular projection but with little change in appearance or thickness of exospore because the lumen projects a short distance into the base of the structure.

Identification of spores and plant affinity

The distinguishing generic features of these spores necessitating assignment to the genus *Synorisporites* are the prominent curvaturae perfectae forming a more or less rigid equatorial

EXPLANATION OF PLATE 1

Figs 1–9. SEMs of spore masses of *Synorisporites downtonensis* Richardson and Lister; Pridoli Series, Welsh Borderland (distal ends to top of plate). 1, NMW95.19G.1; Ludford Corner; $\times 80$. 2, NMW95.19G.2; Ludford Corner; $\times 98$. 3, NMW95.19G.3; Ludford Corner; $\times 80$. 4, NMW95.19G.4; spore mass with incomplete development at presumed proximal end; Ludford Corner; $\times 108$. 5, NMW95.19G.5; anomalous development at base and on left hand side; Ludford Corner; $\times 108$. 6, NMW95.19G.6; bifurcating spore mass; Ludford Corner; $\times 123$. 7, NMW95.19G.7; slender elongate mass with adhering non-cellular material; Weir Quarry; $\times 60$. 8, magnification of one end of 7; $\times 380$. 9, variation in distal ornament in single spore mass illustrated in fig. 3; $\times 450$.



EDWARDS *et al.*, spore masses of *Synorisporites*

crassitude, which is cuneiform in section, and the murornate distal sculpture. Other genera with similar structure are *Ambitisporites* (laevigate), *Streelispora* and *Aneurospora* (apiculate). The spores illustrated here in SEM and TEM are identical to the dispersed spore species *Synorisporites downtonensis*. The nature of the murornate sculpture, particularly on the proximal surface, and the relatively large size of the spores distinguishes this species from all described contemporary *Synorisporites* species. The proximal sculpture was originally described by Richardson and Lister (1969) as having contact areas covered with irregular convolute muri somewhat angular in plan, rounded to conical in profile. It thus differs from the smaller *S. tripapillatus* in the absence of interradian papillae, while *S. verrucatus* lacks proximal muri and possesses verrucate-murate distal ornament. Richardson and Lister isolated *S. downtonensis* from dispersed spore assemblages from Ludford Lane and Downton Gorge (Weir Quarry) but always as monads. However, they recovered similar spores, the best preserved as tetrads, from Lower Ludlow rocks. They called these cf. *S. downtonensis* because they had insufficient information on proximal characters for secure identity. In the light of our study it seems likely that the older spores are conspecific, but were then released into air currents as tetrads rather than monads.

Scanning electron microscopy indicates pronounced differences in both proximal and distal ornament from *Synorisporites verrucatus*, which occurs usually as monads in *Cooksonia pertoni* subsp. *synorispora*, and is also dispersed in discoidal masses. They also differ ultrastructurally, with *S. verrucatus* possessing a bi-layered exospore, the outer layer comprising c. < 20 per cent. of the total wall diameter. *In situ* spores of *S. verrucatus* occur in an inter-spore matrix which includes a peripheral layer around each spore and they lack any evidence of junctions between spores. Thus although the spores described here and those in *Cooksonia pertoni* subsp. *synorispora* are placed in the same spore genus, they derive from plants differing in a number of sporangial characters, including shape. Such plants were probably of differing affinity, and certainly not members of the *Cooksonia* lineage (Edwards *et al.* 1995).

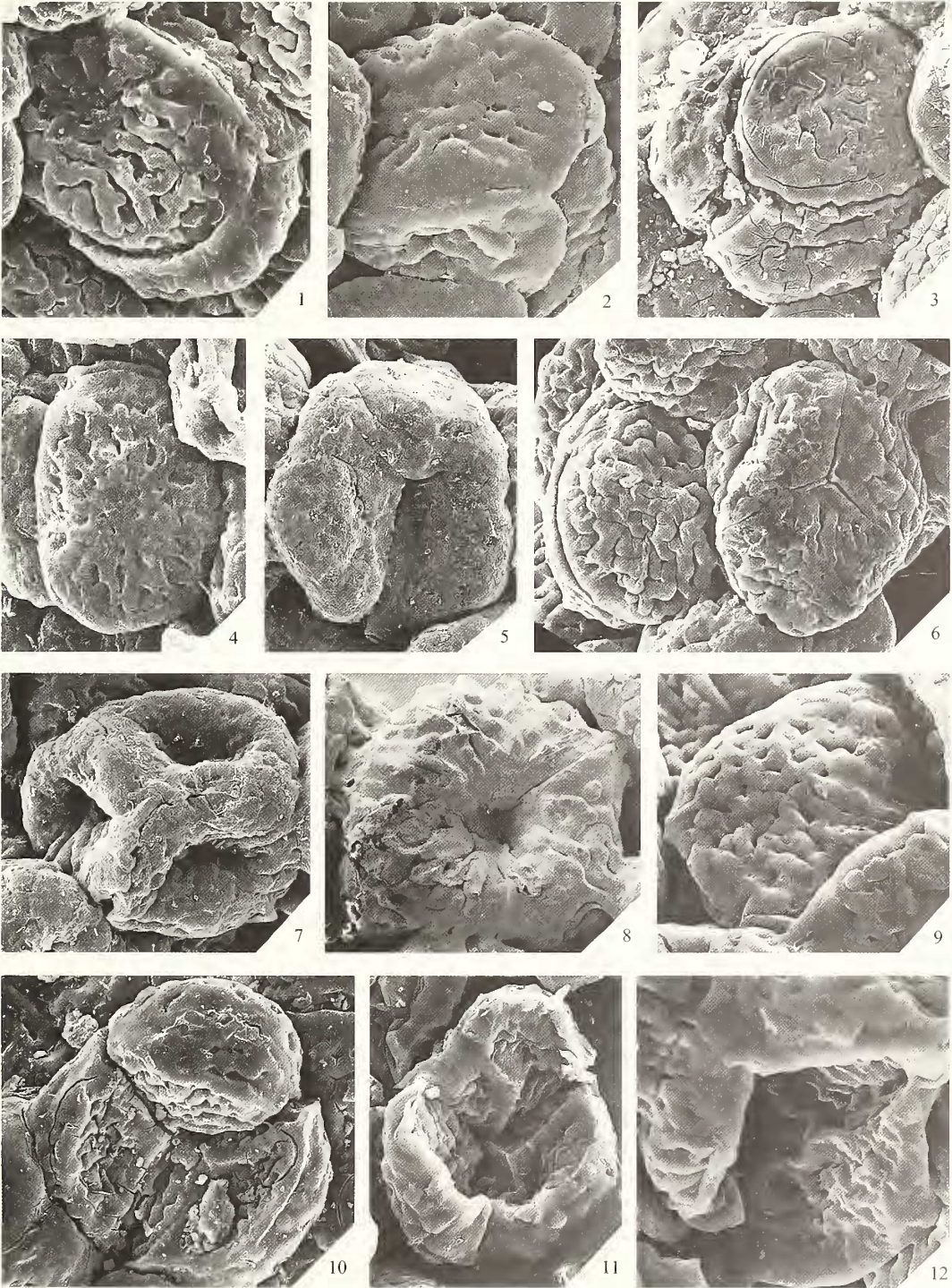
The combination of tetrads, elongate shape, lack of perispore or any indications of tapetal activity in the form of globules preclude relationship with any Upper Silurian and Lower Devonian plant fossils with *in situ* spores yet described (e.g. Fanning *et al.* 1988; Edwards 1996; Edwards and Richardson in press).

Considering broad affinity with higher groups based on extant homosporous plants, the presumed lack of perispore eliminates ferns *sensu lato*, sphenopsids, some homosporous lycopods (Tryon and Lugardon 1991) and mosses, although there is, of course, the possibility that ancient members of a group had different characters from their descendants. The shape of the spore mass is not like that of any fossil or extant Lycopodiales. This leaves the liverworts for more detailed consideration, particularly in relation to trilete marks, persistent tetrads and sporangial shape. Triletes characterize Marchantiales and Anthocerotales, but are not present in taxa such as *Haplomitrium* (Jungerman-

EXPLANATION OF PLATE 2

Figs 1–9. SEMs of *Synorisporites downtonensis* Richardson and Lister, illustrating variation in distal surfaces and equatorial features of spores in tetrads. Fig. 1, Weir Quarry; figs 2–9, Ludford Corner; both Pridoli Series, Welsh Borderland. 1, NMW95.19G.7; $\times 700$. 2, NMW95.19G.6; $\times 825$. 3, NMW95.19G.2; radial stress fractures. These are unlikely to have been produced by beam damage as they are absent from all the other specimens similarly processed; $\times 520$. 4, from the same mass as fig. 2; $\times 700$. 5, NMW95.19G.3; $\times 650$. 6, NMW95.19G.8; $\times 550$. 7, NMW95.19G.3; inward collapse at distal pole; $\times 700$. 8, NMW95.19G.1; collapse at contact between three spores; $\times 600$. 9, NMW95.19G.4; $\times 1000$.

Figs 10–12. SEMs of *S. downtonensis* spores in which one member of the tetrad has become displaced revealing the proximal surfaces of the remaining three. All from Ludford Corner, Pridoli Series, Welsh Borderland. 10, from the same mass as fig. 3; $\times 575$. 11, from the same mass as figs 5 and 7; $\times 625$. 12, from the same mass as fig. 9; $\times 1000$.



niales) where spores adhere in loose tetrads, or in *Sphaerocarpos* (Sphaerocarpaceae) where they do not usually separate. In species that do, there is no trilete mark (Doyle 1975). In some tetrads, components appear to be held together by bridges (e.g. *Sphaerocarpos donnellii*; see Long 1993, fig. 5). Occasional wide bridges between distal surfaces of adjacent spores have been figured in the jungermannialean, *Chandonanthus squarrosus* (Taylor *et al.* 1974). On the basis of shape, the elongate masses of *S. downtonensis* might have derived from an anthocerotalean type of sporangium, but there is no evidence of a columella. Although this structure is absent at maturity in sporangia of certain species of *Anthoceros*, it seems unlikely it was ever present in the masses described here because of the homogeneity of the masses. Thus, by a process of elimination and some disparate similarities, the spore-masses might well have derived from hepatic-like plants where sporangial wall and vegetative tissues lacked the recalcitrant polymers enhancing fossilization potential. In this respect the absence of sporopollenin-impregnated elaters is not critical as they are not universal in liverworts.

Observations on spore development

The significance of the relatively undifferentiated structure of the exospore in terms of affinity is conjectural. While it might well represent the true nature of the exospore at spore maturity, it is also possible that diagenesis has obliterated any substructure, although layering has been observed in different contemporaneous taxa at this and other localities. In most of the spore masses, there is very little variation in spore size and distal ornament throughout the specimen, with persistent connections between tetrads throughout. This seems to indicate synchronous maturation within the sporangium (if sporangial contents are indeed preserved in their entirety). The development of the sporopollenin bridges between ornament on adjacent tetrads is suggestive of polymerization of a final coating of sporopollenin as locular fluid was withdrawn, perhaps accompanied by shrinkage and separation of the tetrads. Whether or not such bridges were mere by-products of development or had the function of holding spores together in the living plant, perhaps ensuring dispersal in clumps, cannot be ascertained. Their absence on tetrads where ornament is marked by sinuous grooves on an otherwise more or less smooth surface, suggests that the distal ornament was formed by a final phase of sporopollenin deposition on a template possibly initiated by the sporocyte or more probably the spore. In the specimen lacking pronounced ornament (Pl. 2, fig. 3), proximal surfaces of the spores are still in contact although not linked. The circular fractures mentioned earlier and small 'crazed' fractures not seen on other specimens suggest different properties of the wall prior to fossilization. That these tetrads are larger than the others might be seen as evidence against an immaturity hypothesis. It is however possible that the spores shrank during the final phase of sporopollenin development, and as they did so produced the bridges. The gametophytic control element of the hypothesis appears to find some support in three specimens where atypical

EXPLANATION OF PLATE 3

Figs 1–12. SEMs of *Synorisporites downtonensis* Richardson and Lister; Ludford Corner, Pridoli Series, Welsh Borderland. 1–3, proximal surfaces. 1, NMW95.19G.9; $\times 825$. 2, NMW95.19G.4; $\times 1075$. 3, NMW95.19G.3; note flattened areas in interradian region at pole; $\times 875$. 4–6, regions of spore masses showing incomplete development of tetrads which are often linked by broad bands of sporopollenin. 4, NMW95.19G.5; $\times 270$. 5, NMW95.19G.5; possible wall fragment is arrowed; $\times 320$. 6, NMW95.19G.3; $\times 380$. 7, NMW95.19G.1; bridges between proximal faces of members of same tetrad; $\times 1100$. 8, NMW95.19G.3; indistinct bridges (top left) between adjacent tetrads where distal ornament is poorly developed; $\times 825$. 9, NMW95.19G.8; prominent bridges between adjacent tetrads with well-defined ornament; $\times 590$. 10, as for 9, NMW95.19G.4; $\times 1200$. 11, NMW95.19G.4; pyrite damage on incompletely developed spore; $\times 2100$. 12, NMW95.19G.4; broad bridge between spores with incompletely developed ornament; $\times 675$.

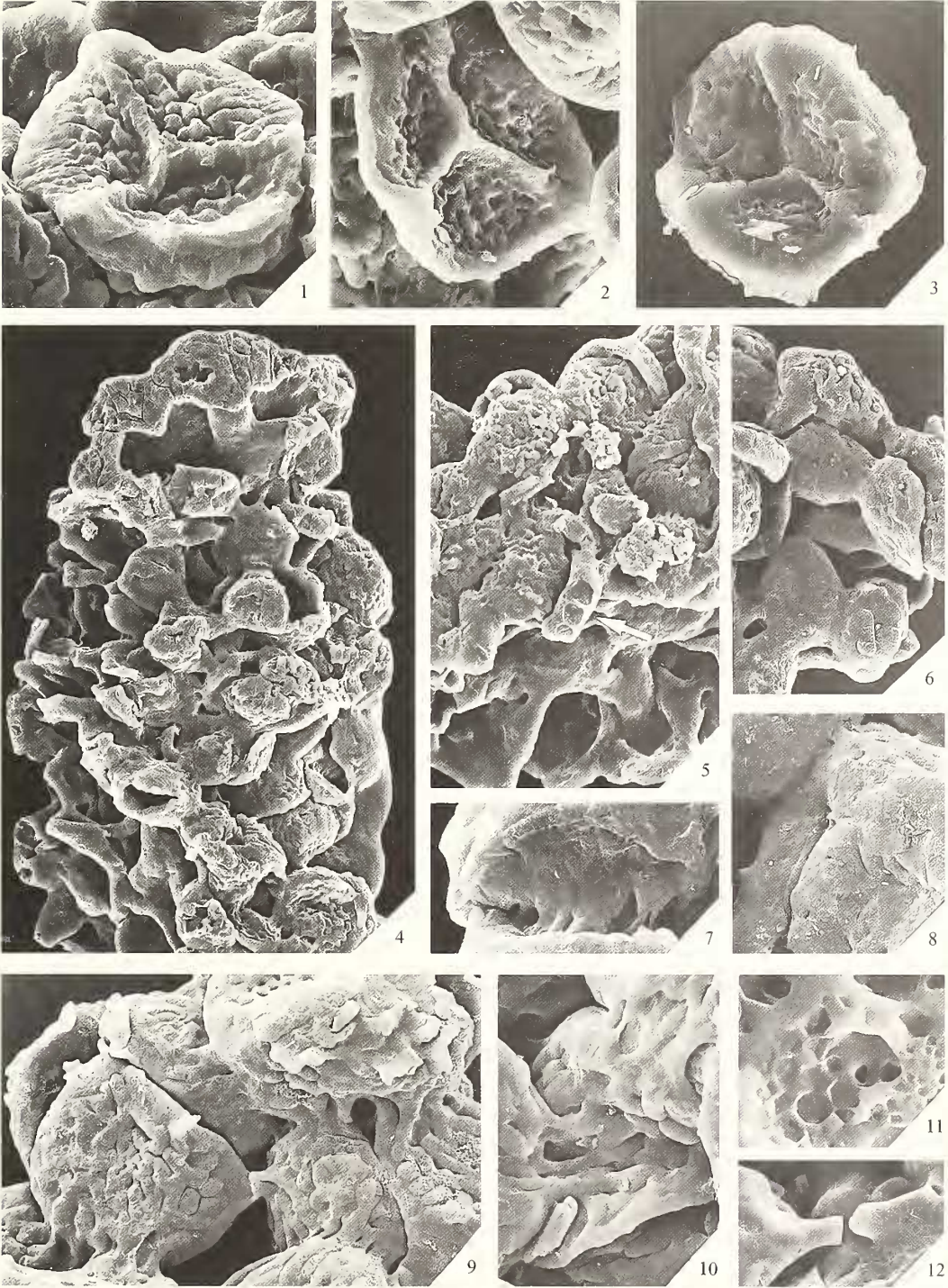
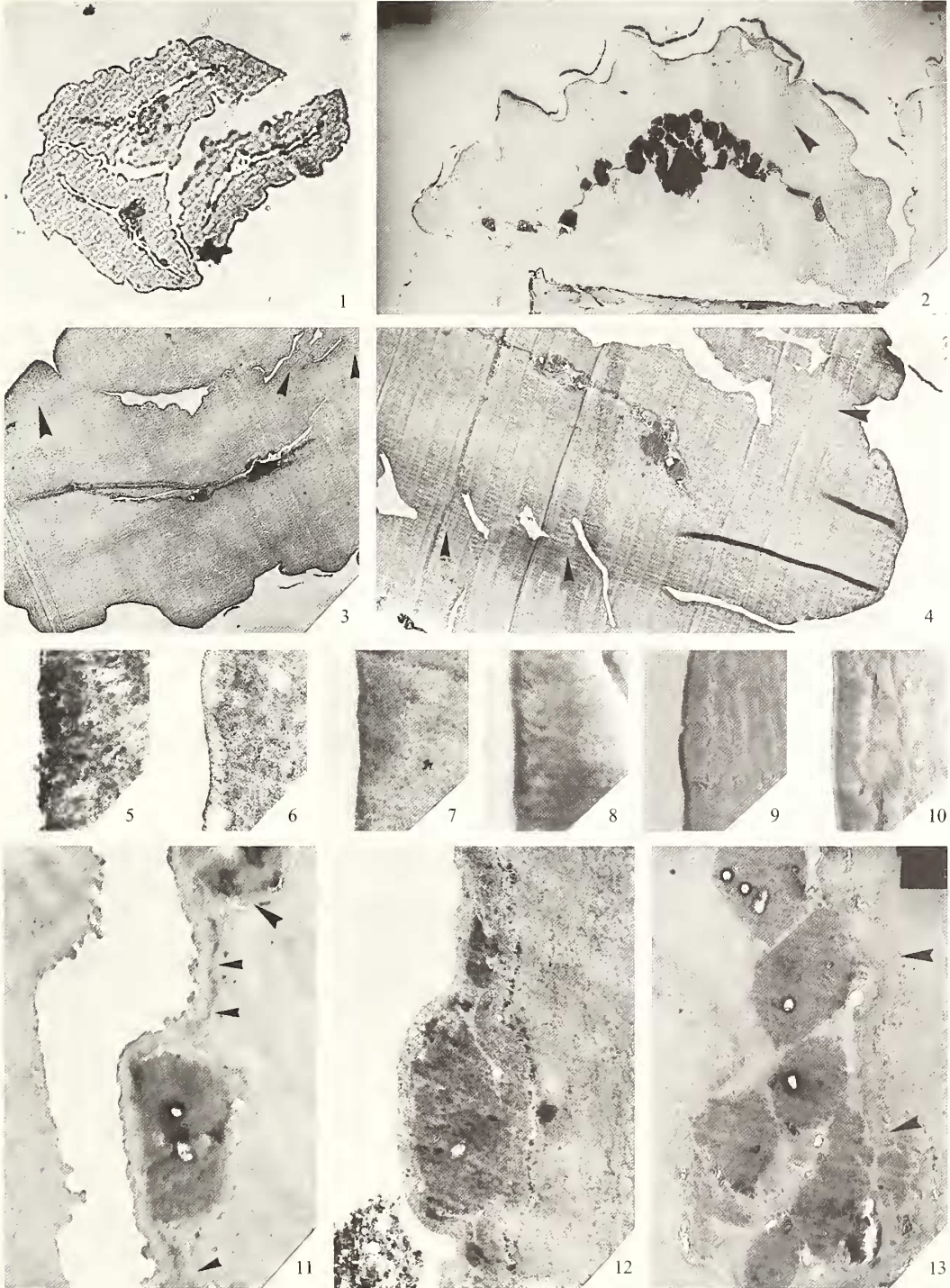


TABLE 1. Data for spore masses comprising *Synorisporites downtonensis*. All from Ludford Lane except NMW95.19G.7 (Weir Quarry)

| Specimen number | Length of spore mass (μm) | Width of spore mass (μm) | + / - Forked | Monad dimensions (μm) | Tetrad dimensions (μm) | c. No. of tetrads in spore mass |
|-----------------|--|---------------------------------------|--------------|------------------------------------|-------------------------------------|---------------------------------|
| NMW95.19G.3 | 1170 | 289 | - | 40 (48) 55, N = 13 | 58 (66) 76, N = 20 | 375 |
| NMW93.143G.8 | 915 | 215 | - | 44 (53) 59, N = 13 | 62 (71) 80, N = 20 | 181 |
| NMW95.19G.1 | 1180 | 220 | - | 48 (54) 63, N = 11 | 65 (78) 86, N = 20 | 132 |
| NMW95.19G.9 | 850 | 220 | - | 49 (55) 60, N = 13 | 66 (74) 81, N = 11 | 113 |
| NMW95.19G.5 | 790 | 250 | - | 50 (53) 55, N = 7 | 64 (72) 87, N = 12 | 147 |
| NMW95.19G.6 | 580 | 158 | + | 50 (55) 59, N = 12 | 56 (68) 78, N = 16 | 62 |
| NMW95.19G.8 | 543 | 183 | - | 55 (58) 60, N = 10 | 63 (74) 83, N = 16 | 50 |
| NMW95.19G.4 | 825 | 226 | - | 40 (43) 49, N = 19 | 51 (59) 68, N = 20 | 228 |
| NMW95.19G.7 | 1490 | 207 | - | 53 (58) 62, N = 11 | 62 (72) 83, N = 12 | 192 |
| NMW95.19G.2 | 957 | 260 | - | 52 (59) 65, N = 8 | 75 (85) 93, N = 6 | 117 |
| NMW95.19G.12 | 960 | 240 | - | 54 (59) 62, N = 4 | 63 (77) 82, N = 15 | 134 |
| NMW95.19G.13 | 945 | 220 | - | 54 (59) 63, N = 3 | 67 (72) 82, N = 10 | 89 |

EXPLANATION OF PLATE 4

Figs 1-13. *Synorisporites downtonensis*; figs 1 and 10 Weir Quarry (NMW95.19G.7); remainder Ludford Corner (NMW93.143G.8); both Přídolí Series, Welsh Borderland; all nitric acid treated. 1, LM of section through three of four members of a tetrad. Note ridges marking arms of trilete, $\times 610$. 2-13, TEMs. 2, section through complete spore with thicker distal wall (arrow). Electron-dense bodies occupy lumen. Detached dark line represents gold coating. Note differences in contours of distal and proximal surfaces; $\times 1435$. 3, walls of two adjacent spores with junction between proximal faces (small arrows). Note increase in thickening at margin of proximal wall (large arrow) in spore where distal wall also present; $\times 2470$. 4, bridges (arrows) between distal surfaces of adjacent spores, and at margin of proximal face (large arrow); $\times 3260$. 5-10, variation in appearance of outermost part of distal wall. 5, $\times 15000$. 6, $\times 12500$, 7, $\times 20200$. 8, $\times 20000$. 9, $\times 10000$. 10, $\times 15000$. 11-13, sections through lumen region following nitric acid treatment. 11, large lighter area is space resulting from the breakage of a discontinuous layer marked by arrows on the intact side; $\times 18000$. 12, as for 11 with additional darkly staining granules at the line of weakness; $\times 17300$. 13, larger densely staining bodies in light amorphous matrix, bordered by slightly darker layer separated from rest of exospore by a row of small irregular voids (arrows: large arrow in 11); $\times 11000$.



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tetrads are present. Typical tetrads occur at the attenuated (?intact) apex, but collapsed, fragmentary or poorly defined tetrads occur elsewhere. In some cases these spores show weakly defined distal ornament (Pl. 2, figs 2, 5, 7) and may have collapsed centripetally producing a hollow spherical structure (Pl. 2, fig. 11). In other examples, ornament or, in some cases, even the rounded outline of a spore cannot be detected and the tetrads are replaced by interconnecting straps or sheets (Pl. 3, figs 4–6). The latter sometimes bear the imprint of pyrite crystals (Pl. 3, fig. 11) perhaps indicating that the sporopollenin impregnated wall was softer when the mass was fossilized. The one specimen (Pl. 1, fig. 4) where such spores are concentrated at one end might provide evidence for continued meiosis and spore production at the base of a sporangium, as occurs in extant *Anthoceros*. However, in the two other cases the region of abnormal tetrads extends along one side of the mass and is probably more indicative of meiotic failure. This suggests that all the sporangial contents, whether ?sporocytes, aborted spores or fully developed tetrads, were coated in the final phase of sporopollenin deposition. If the verrucate patterning had been determined by the sporophyte, as in extant liverworts (Brown *et al.* 1986), it would be expected to have been present on the incompletely developed spores, as has been shown in extant angiosperms where 'normal' patterning occurs on aborted pollen (e.g. Tischler 1908). However, based on his very detailed studies on exine and exospore development, J. R. Rowley (Stockholm) considers it very unlikely that 'changes in exine form continue following the death of the microspore' (pers. comm. 1995; Rowley and Flynn 1969). The abnormal spores and fragments described here, with their unornamented walls, support such an interpretation of gametophytic control.

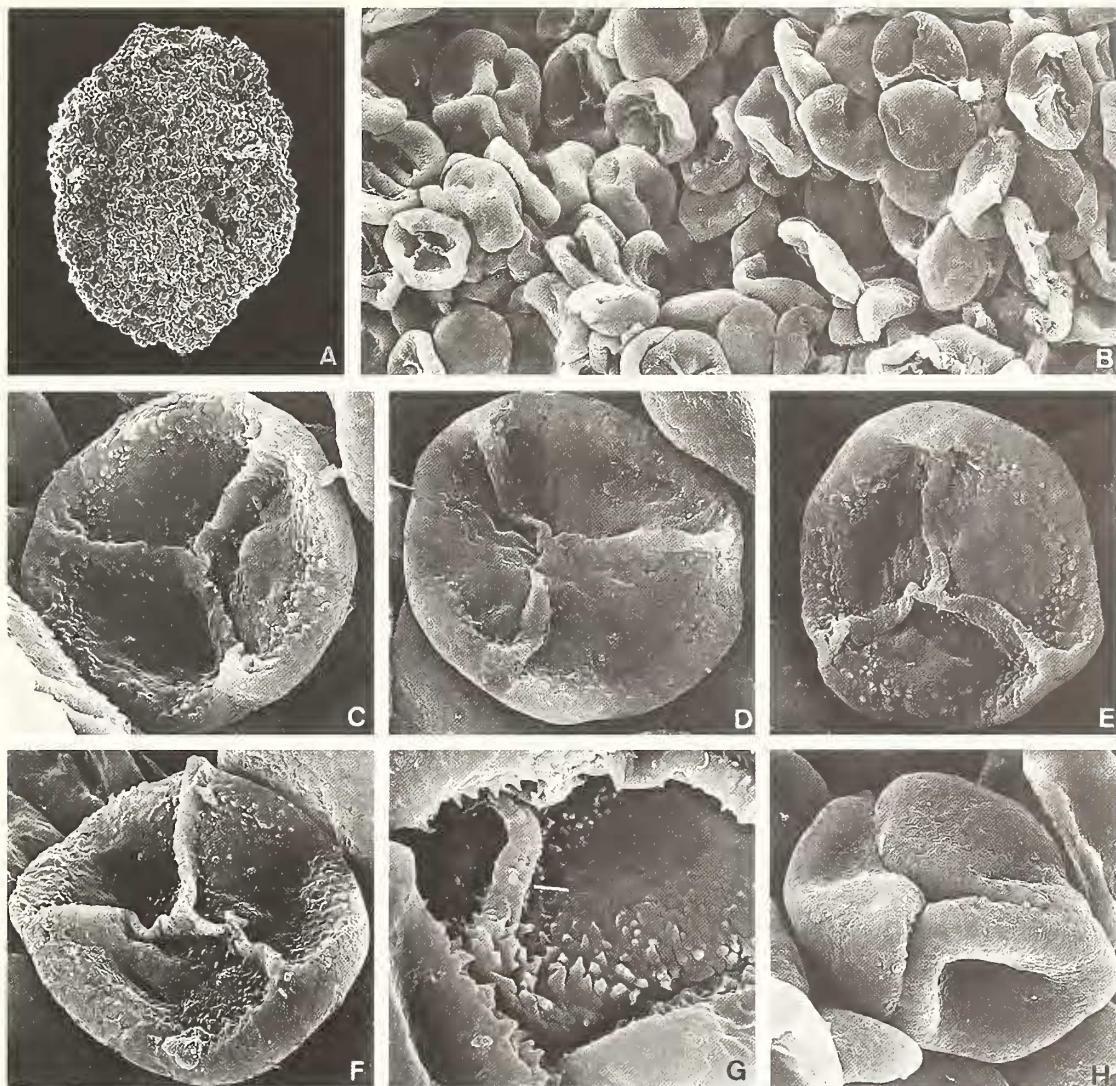
SPORE MASSES WITH *RETUSOTRILETES* CF. *CORONADUS*

Description

SEM observations. Spores of similar morphology to those in the two masses described here, but of greater diameter, were recorded in sporangia of *Pertonella dactylethra* from Perton Lane. One of the spore masses (Text-fig. 2A) from the same locality is discoidal and of such dimensions (0.94 mm × 0.68 mm) that it probably represents the entire contents of a single sporangium of *P. dactylethra*. The other is less regular in shape, and spores have more pronounced proximal ornament. Neither has any indications of the sporangial wall, nor of any extrasporal material. Dimensions of sporangial masses and spores are given in Table 2.

The spores have a circular to subcircular amb (Text-fig. 2B). The exospore is rigid, but often invaginated over the proximal surface (Text-fig. 2E). Trilete folds are prominent, sinuous, almost reach the equator and often bear grana and microconi scattered on the folds and forming bands (1–4 µm wide) on the flanking proximal exospore on both sides of the trilete folds (Text-fig. 2C–F). At or near the radial apices the trilete folds and their sculptural bands coalesce with a sculptured zone forming proximal and subequatorial curvaturae perfectae; bands (3–4 µm wide) comprise minute sculptural elements; curvatural and proximal sculptural elements, ± isodiametric (< 1 µm), consist of grana, microconi and microbaculae (Text-fig. 2G). Distal (Text-fig. 2H), equatorial and proximal triangular areas (between curvaturae and trilete sculptural bands) are laevigate.

TEM observations. Sections taken from the discoidal spore mass are noteworthy in showing a minimum of sectioning artefacts. Unlike in *Synorisporites downtonensis* there are major differences in appearance after nitric acid treatment which obliterates the layering typical of untreated specimens as seen in Plate 5, figure 1. In this almost complete section, the distal wall is of more or less uniform width, thicker than the proximal and laevigate on the surface, while the proximal is thinnest in the region of the apertural fold (c. 30 per cent. of the width of the opposing distal wall) and increases in thickness towards the equator. This variation in thickness results in a caving inwards of the central area of the proximal wall, a phenomenon also noted in the SEMs (Text-fig.



TEXT-FIG. 2. SEMs of spore mass (A: NMW95.19G.10) and its contained spores (B-H), which are assigned to *Retusotriletes* cf. *coronatus*, Perton Lane, near Hereford, Welsh Borderland; Přídolí Series. All, except E, untreated with nitric acid. A, $\times 46$; B, $\times 610$; C-F proximal surface. C, $\times 2050$; D, $\times 1900$; E, $\times 1950$; F, $\times 1900$; G, ornament on proximal surface, trilete fold arrowed, $\times 3900$; H, three members of a tetrad, $\times 1375$.

TABLE 2. Data for spore masses comprising *Retusotriletes* cf. *coronatus* from Perton Lane, Přídolí Series.

| Specimen number | Length of spore mass | Width of spore mass | Spore dimensions (μm) |
|-----------------|----------------------|---------------------|------------------------------------|
| NMW95.19G.11 | 860 μm | 680 μm | 20 (24) 30, $N = 18$ |
| NMW95.19G.10 | 940 μm | 680 μm | 20 (22.5) 27, $N = 20$ |

2C–F). Both proximal wall and apertural fold bear occasional, irregularly sized and distributed cones (Text-fig. 2C–G). At low magnifications, the lumen appears bounded by a dark line and contains intensely staining, discrete rounded or oval bodies or rounded to oval bodies. At higher magnification, in some sections, the boundary layer is further resolved into a dark line and inner layer with irregular inner limit (Pl. 5, fig. 4) immediately adjacent to the lumen. In others the darker layer fades into the rest of the exospore, but internally is continuous with very disorganized, almost fibrillar, material within the lumen where it may also partially encase the very electron-dense bodies (Pl. 5, fig. 5). The rest of the spore wall may appear homogeneous (Pl. 5, fig. 4) or show traces of very faint striations (Pl. 5, fig. 5).

The darker layer around the lumen enters the base of the apertural fold (Pl. 5, figs 1–2) and extends into it as diffuse lines (Pl. 5, fig. 3), indicating that the wall of the fold is of similar width to the immediately adjacent proximal wall.

None of this layering is visible after nitric acid treatment (Pl. 5, figs 2, 7), and a reticulum in the lumen marks the original position of the darkly staining bodies (Pl. 5, figs 1–2). In some areas there is a faint indication of spongy texture in the innermost part of the wall itself (Pl. 5, fig. 7).

We have no information on the nature or composition of the dark bodies: the fibrillar material surrounding them might represent the remains of cell contents, although its continuity with the exospore is puzzling. The darker lines which disappear on acid treatment might represent the coalified residues of cellulose, perhaps part of the endospore. Equally conjectural are the origins of the faint striations parallel to the exospore surface, in that they could represent a compressed multifoliate structure, possibly even the vestiges of the lamellae seen in certain fossil and extant lycophyte spores (Tryon and Lugardon 1991) and in liverworts (Brown *et al.* 1986).

IDENTIFICATION OF SPORES AND PLANT AFFINITY

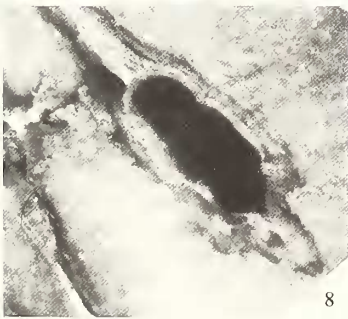
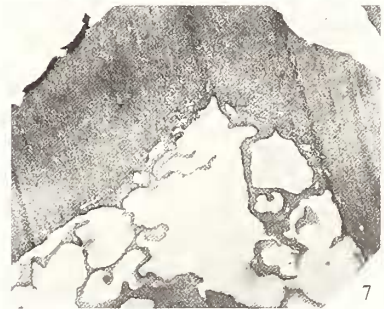
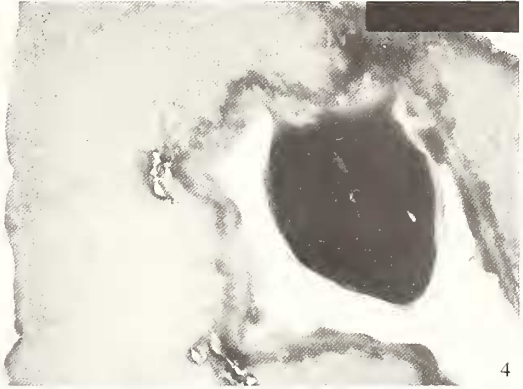
When originally describing the spores extracted from *Pertonella dactylethra* (Fanning, Edwards and Richardson 1991), it was noted that they resembled one of the spores illustrated in the paper containing the original description of *Retusotriletes coronadus* Rodriguez Gonzalez, 1983 which

EXPLANATION OF PLATE 5

Figs 1–10. TEMs of *Retusotriletes cf. coronadus*; NMW95.19G.10; Perton Lane, Pridoli, Welsh Borderland.

1, almost entire spore before acid treatment, trilete fold is arrowed; $\times 5500$. 2, spore after acid treatment; trilete arrowed; note absence of dark bodies in lumen; $\times 3260$. 3, magnification of trilete fold in fig. 1; $\times 25000$. 4, area of spore, before acid treatment, showing position of lumen (light area); electron-dense body partly surrounded by narrow layer and layering to inside of the exospore; $\times 25000$. 5, proximal (light) and distal walls of same spore before acid treatment; darker staining areas around lumen may indicate layering of exospore or adressed spore contents; note ornament on outer edge of thinner proximal wall and possible layering in exospore; $\times 28400$. 6, magnification of 5 to show ornament on the proximal surface with some indication of lamellae in the exospore; $\times 50000$. 7, part of spore after nitric acid treatment showing network in lumen (marking original position of darker bodies) which appears continuous with the rest of the exospore; innermost region of exospore below apertural fold has spongy appearance; $\times 5780$. 8, compressed lumen filled by dark body surrounded by lighter region, with layering to inside of exospore, before acid treatment; $\times 20450$. 9, ornament on proximal surface; $\times 25000$. 10, higher magnification of inner part of exospore, showing layering adjacent to lumen; $\times 43750$.

Fig. 11. TEM of *Synorisporites downtonensis* Richardson and Lister; NMW93.143G.8; Ludford Corner, Pridoli Series, Welsh Borderland; two adjacent spores of a tetrad showing fusion of proximal surfaces (arrow) and wedge-shaped equatorial region (*), after nitric acid treatment; $\times 910$.



occurs in dispersed assemblages from the Lower Devonian of Spain and is identified as *R. coronadus* in the figure legend. The *in situ* *Pertonella* spores did not exactly conform with the illustrated holotype nor to the diagnosis of that species and consequently the specific prefix 'cf.' was used in 1991.

Dispersed spores almost identical to the *in situ* spores from *P. dactylethra* are relatively common in the matrix at Perton Lane (Fanning, Edwards and Richardson 1991) and, following re-examination of the type material for *R. coronadus*, will probably be placed in a new species of *Retusotriletes* (JBR, work in progress). However, the *in situ* spores are larger (34 (39) 45 μm : 20 specimens measured), than the dispersed specimens (14 (22) 36 μm : 44 specimens measured). The spores described in this paper are almost identical to those extracted from the coalified compression fossils of *P. dactylethra* from the same locality but are smaller and are more similar in size to the dispersed examples.

In considering broad affinities, the arguments rehearsed for the *Synorisporites downtonensis* spore masses are equally relevant here, particularly as regards the lack of any peripheral material, and hence presumably perispore. However, in this case the spores are contained in sporangia that terminate naked dichotomously branching axes. In that it has not been possible to demonstrate tracheids, such plants are called rhyniophytoid, but are probably tracheophytes. Sporangial shape is identical with that of the tracheophyte *Cooksonia pertoni* and, although the sporangial spines might be considered a specific character, Fanning, Edwards and Richardson (1991) decided to place the Perton Lane fossils in a new genus because of their highly distinctive retusoid spores. These ultrastructural studies, in failing to demonstrate peripheral material or the bilayered exospores typical of *Ambitisporites* – *Synorisporites verrucatus* – *Streelispora newportensis*/*Aneurospora* in the *Cooksonia pertoni* lineage, further justify that decision. *Pertonella* is not closely related to *Cooksonia*. Absence of extrasporal layers hints at affinity with certain homosporous lycophytes (Tryon and Lugardon 1991) but unfortunately there is no information on spores of approximately coeval examples (sometimes called prelycophytes) such as *Drepanophycus*, *Baragwanathia* and *Asteroxylon* (Gensel 1992; Hueber 1992; Li and Edwards 1995). In this context it is perhaps relevant that Hueber (1992) has suggested that both zosterophylls and lycophytes had their origins in a plexus of cooksonioid plants (cooksonioid here referring to sporangial shape) and that the two groups became separate somewhere between the 'late Early Silurian and the early Lower Devonian'. In this scenario the sporangial spines in *Pertonella* (a cooksonioid on Hueber's definition) provide evidence for a novel hypothesis for the evolution of the lycophyte leaf, i.e. that the enation was first produced on a sporangium and that the microphyll, a vascularized enation, eventually resulted from precocious development of such enations on vegetative axes (Bower 1935; Edwards 1993).

CONCLUSIONS

The kinds of comparisons employed here – the palaeobotanical taxonomist's equivalent of clutching at straws – emphasize the major dilemma in attempts to classify early land plants. Available characters are few and the plants so simple morphologically that homoplasy probably abounds. Our studies show that spores have some value in providing additional characters, but that their full potential will not be realized until we have more information on modern and fossil taxa (particularly bryophytes), a greater understanding of spore and sporangial development in extant forms, elucidation of the effects of diagenesis on spore ultrastructure and, of course, more fossils with *in situ* spores.

Acknowledgements. We thank E. C. W. Rogerson for provision of some of the spore masses, and the NERC (GR3/6708: Una Fanning, 3/7882: KLD and 9/01441) and the Leverhulme Trust (CW and DE) for financial support.

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Typescript received 2 May 1995

Revised typescript received 3 November 1995